Palaeogeography, Palaeoclimatology, Palaeoecology, 15(1974): 267—290

MARINE BIVALVES: DISTRIBUTION OF MERO-PLANKTONIC SHELL-BEARING LARVAE IN EASTERN NORTH ATLANTIC SURFACE WATERS

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(Accepted for publication May 8, 1974)

ABSTRACT

Thiede, J., 1974. Marine bivalves: distribution of mero-planktonic shell-bearing larvae in eastern North Atlantic surface waters. Palaeogeogr., Palaeoclimatol., Palaeoecol., 15: 267—290.

Larval shells of benthic marine bivalves occur frequently in plankton samples from temperate to tropical eastern North Atlantic waters. At many sites their abundance is higher than fifty specimens per cubic meter of surface water, thus outnumbering the other planktonic components with calcareous shells. Generally they are more frequent in nearshore water masses than far from land, but it could be shown that not only faunas on continental shelves, but also on oceanic inlands and on submarine elevations, produce larvae, which can be found far out in the ocean.

Although it cannot be excluded that long-transported bivalve larvae have also been found in these samples, two arguments seem to assure that the bulk of these shells has been produced in the neighbouring shallow-water areas: decreasing abundance as well as increasing size of shells with increasing distance from the shallow-water area (this applies both to island and continental shelves).

The bulk of bivalve shells is concentrated in surface waters. However, shells have also been found with decreasing abundance in water depths down to 600 m. The size distribution in the water column is qualitatively similar for water masses close to the coast and far from land; large shells occur in the upper 50 m, but average diameter decreases below this depth. However, far from land in water depths of 500—600 m they can reach sizes up to about 0.5 mm in diameter (according to one specimen). Generally, shell sizes are larger in corresponding water depth levels far from than in those close to land.

The occurrence of larval shells of bivalves throughout the eastern North Atlantic also has wide paleogeographic implications. Since no specific determinations of these bivalves have been tried, it is unknown in which water depths their parental generations occur. However, it can be assumed that eastern North Atlantic island shelves and peaks of submarine guyots and other subsurface elevations which reach to within a few hundred

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meters of the surface, can be populated by faunas from eastern Atlantic continental margins being transported by off-shore currents far into the ocean. Since the islands and presumably guyots, etc. as well, produce pelagic larval assemblages from their own benthic molluscan faunas, it can easily be assumed that larval shells can be transported across the ocean by surface and subsurface currents.

INTRODUCTION

In plankton samples taken during cruise no. 25 of R/V "Meteor" to the eastern North Atlantic off West Africa, the calcareous shells of larval stages (veliger) of molluscs which usually live as benthos on the bottom of the sea (or attached to a suitable substrate), were found. In many samples they occur more abundantly than the shells of foraminifera and pelagic living gastropods which are usually assumed to be the classsic planktonic living organisms with calcareous shells. It seems therefore difficult to understand that this group has been neglected by geologists for such a long time, since the tests and skeletons of larval mollusc stages are important contributors of calcareous matter to the sediments of shelves and upper continental slopes if they are not destroyed before final sedimentation. In the past they have rarely been described as a distinct group. In many areas they are seldom found, presumably because their shells are fragile and only little resistant to $CaCO_3$ dissolution. The actual shell material used by these larvae for their shells has not yet been determined, partly because their systematic position is not clear (compare Bøggild, 1930, and discussion in Revelle and Fairbridge, 1957). However, their shells are expected to play an important role in the carbonate cycle of the water masses of tropical ocean/continental margin areas because in these areas their abundance is at least as high as that of foraminifera or pteropods.

In the neighbourhood of shelf areas mollusc larvae are frequently found, and here because of their abundance, they have to be included in calculations of the $CaCO_3$ cycle of sea water. Similarly to the aragonitic shells of pelagic gastropods, they are rarely found in deep sea sediments and deposits on the continental margins (Diester-Haass et al., 1973, Kudrass, 1973), presumably because they are destroyed or dissolved before being covered by sediment.

The fact that many benthic living molluscs have a pelagic larval stage is paleogeographically of the utmost importance. Most of these larval stages can

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PLATE I

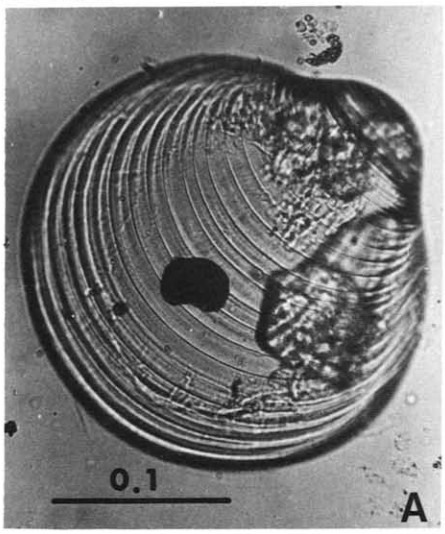
Typical examples of bivalve shells found in plankton samples from surface water masses. The pictures were taken on board R/V "Meteor" (Utermöhl-microscope, flashlight, scales in mm, position of A, C, D, E: 16°46.1′N 22°01.0′ W, position of B: 16° 11.6′ N 22° 20.7′W.

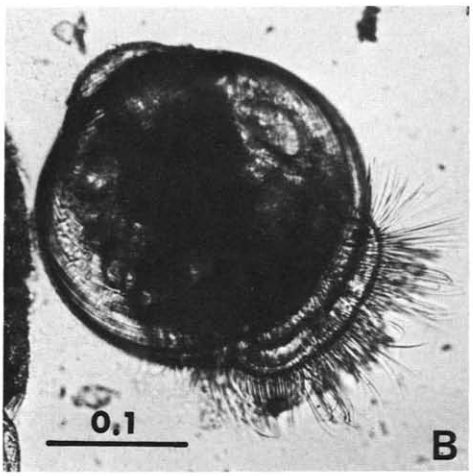
A. Empty shell.

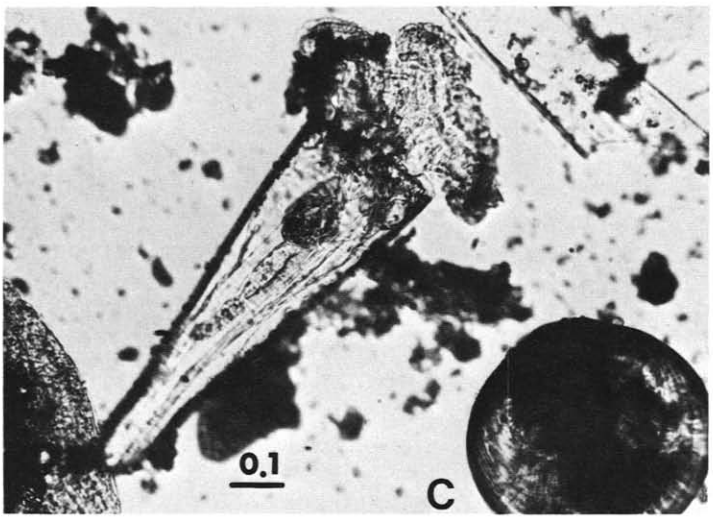
B, D. Living double-shelled specimens.

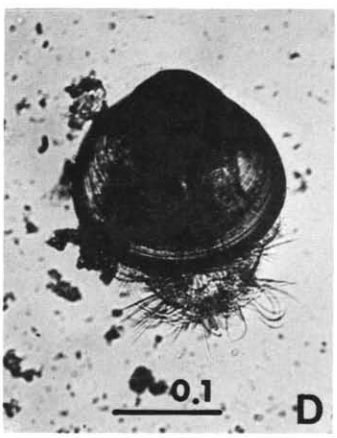
C, E. Typical examples of plankton assemblages (size $>$ 0.12 mm) found in eastern North Atlantic surface waters. Besides bivalves, shell- and skeleton-bearing components consist mostly of radiolaria, foraminifera, pelagic gastropods. However, pelagic crustaceans are extremely frequent in most samples.

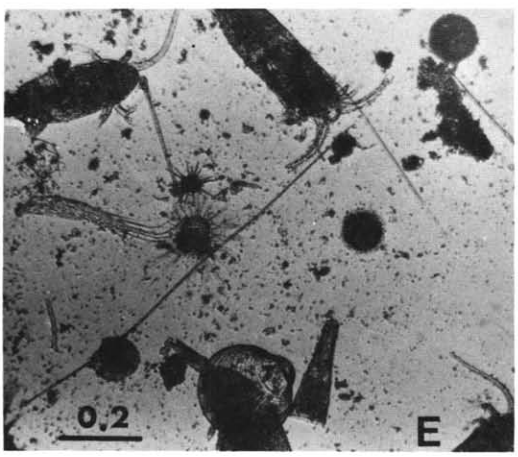
PLATE I











live several weeks (primarily three weeks, according to Thorson, 1946, 1950) close to the sea surface and they can thus be transported by currents over long distances. For example Strauch (1972) describes distribution paths of some bivalve species which develop pelagic larvae, during Tertiary and Quaternary times in the Northern Hemisphere. The similarity between mollusc faunas on both sides of the Atlantic and their settlement on submarine mountains located close to the sea surface but situated far from land are important factors in this pattern. Finally, the development of pelagic larvae allows mollusc populations or faunas of a shallow-water benthos community to cross oceans without any land bridge. Since mollusc faunas are dependent on climate, one can define a number of climatic zones based on them. Their boundaries coincide with certain surface water isotherms, thus the pelagic larvae of these faunas are presumably very good indications of their source. However, the exact origin of the larvae cannot always be proven. Scheltema (1966) describes the trans-Atlantic transport of larvae of a gastropod. If these species are found on both sides of the Atlantic, larvae can be produced on both sides also. Some paragraphs of this discussion will therefore deal with possibilities to prove the area of origin of mollusc larvae.

The above-mentioned problems will be discussed in this paper using bivalve larvae which have been found frequently in the plankton samples described here (both living specimens and empty shells; compare Plate I). Although it seems very difficult, if not impossible, to identify these larvae to the species level, they have the advantage of occurring frequently in many samples, and also, their size can be easily measured. It seems important for geologists to learn more about the occurrence and distribution of these larvae because of their frequency in upper continental slope sediments (Kudrass, 1973).

The samples which have been available for this study come chiefly from surface waters, except very few vertical plankton multiple net tows. They have been taken only during one season of the year (autumn) which seems to be a disadvantage for their general interpretation (compare data from Seguin, 1966). On the other hand, they cover a geographically large area and several climatic zones (lusitanic to tropical, humid—semiarid—arid, upwelling—not upwelling, etc.), and it was therefore hoped that they would mirror these regional differences.

METHODS OF STUDY

The samples mentioned in this paper have been taken during cruise no. 25 of the German R/V "Meteor" in October to December, 1971 (compare cruise report of Seibold, 1972) which crossed eastern North Atlantic waters down to West Africa. The northernmost samples were taken from the mouth of the English Channel to the Bay of Biscay, the southernmost ones off Dakar, Senegal (compare Figs. 1, 2A).

Since special emphasis has been given to the continental margins of West

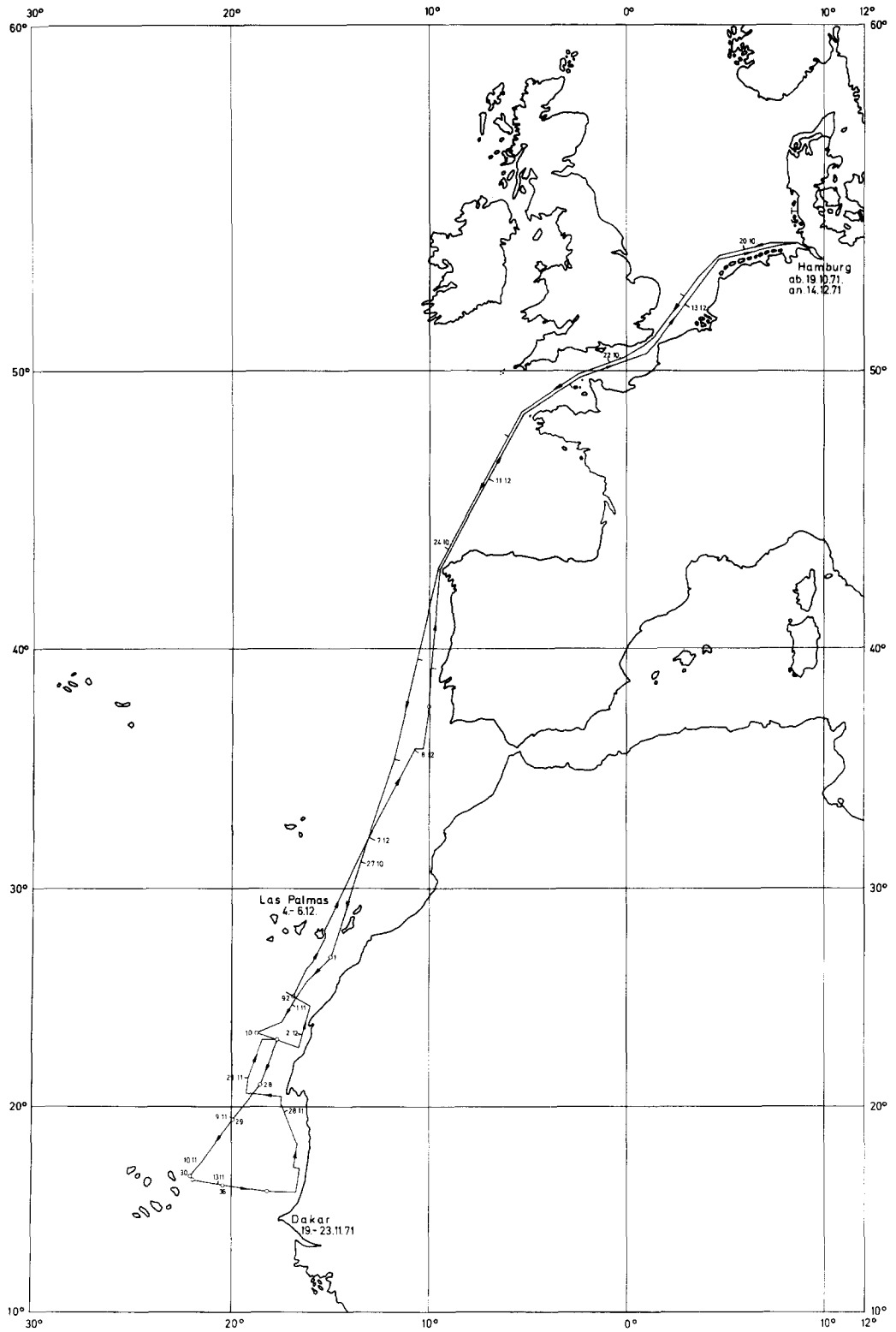


Fig.1. Map of surveyed area and generalized courses of "Meteor" cruise no. 25 in October—December 1971.

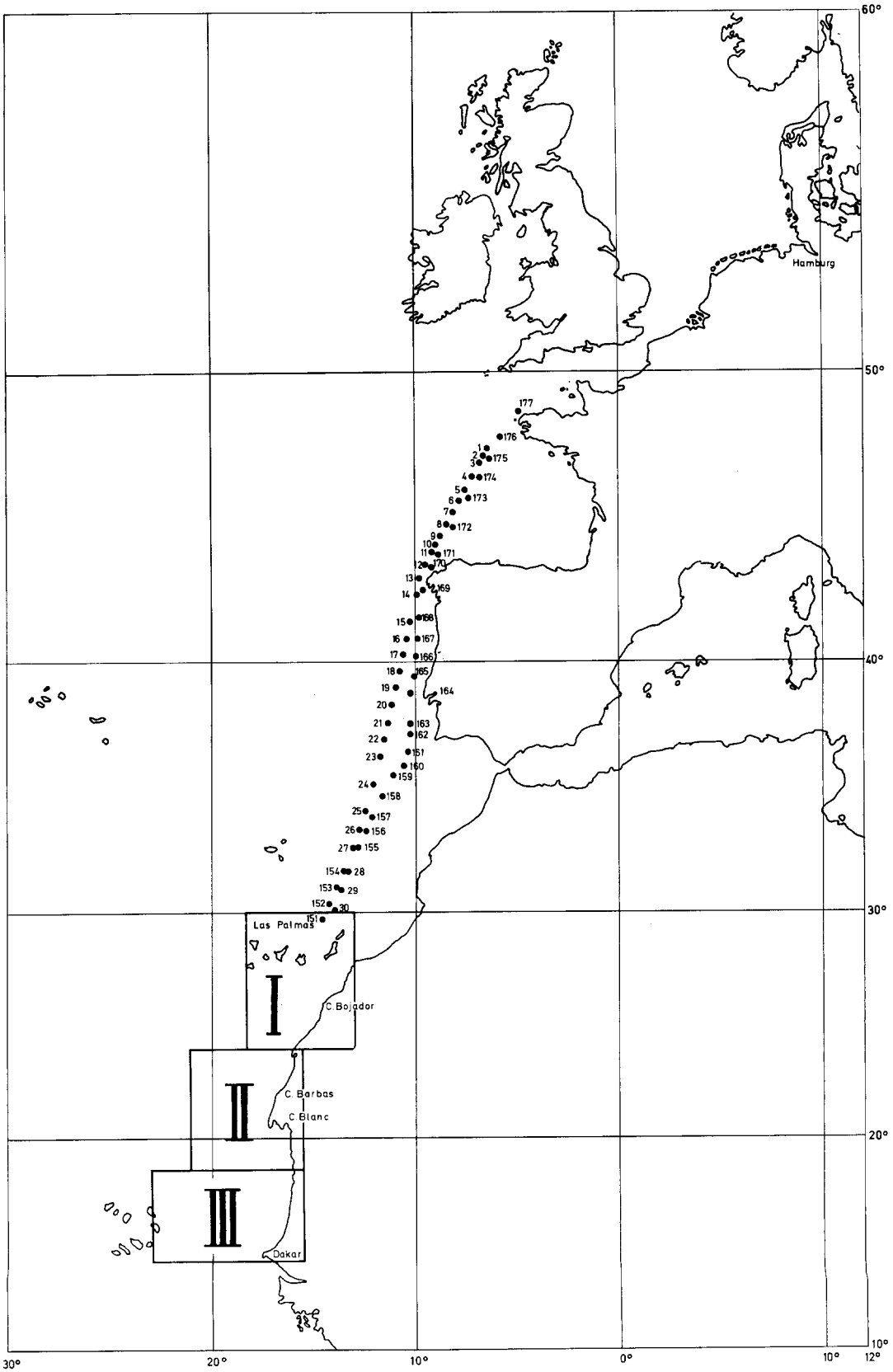


Fig. 2A. (Legend see p. 276.)

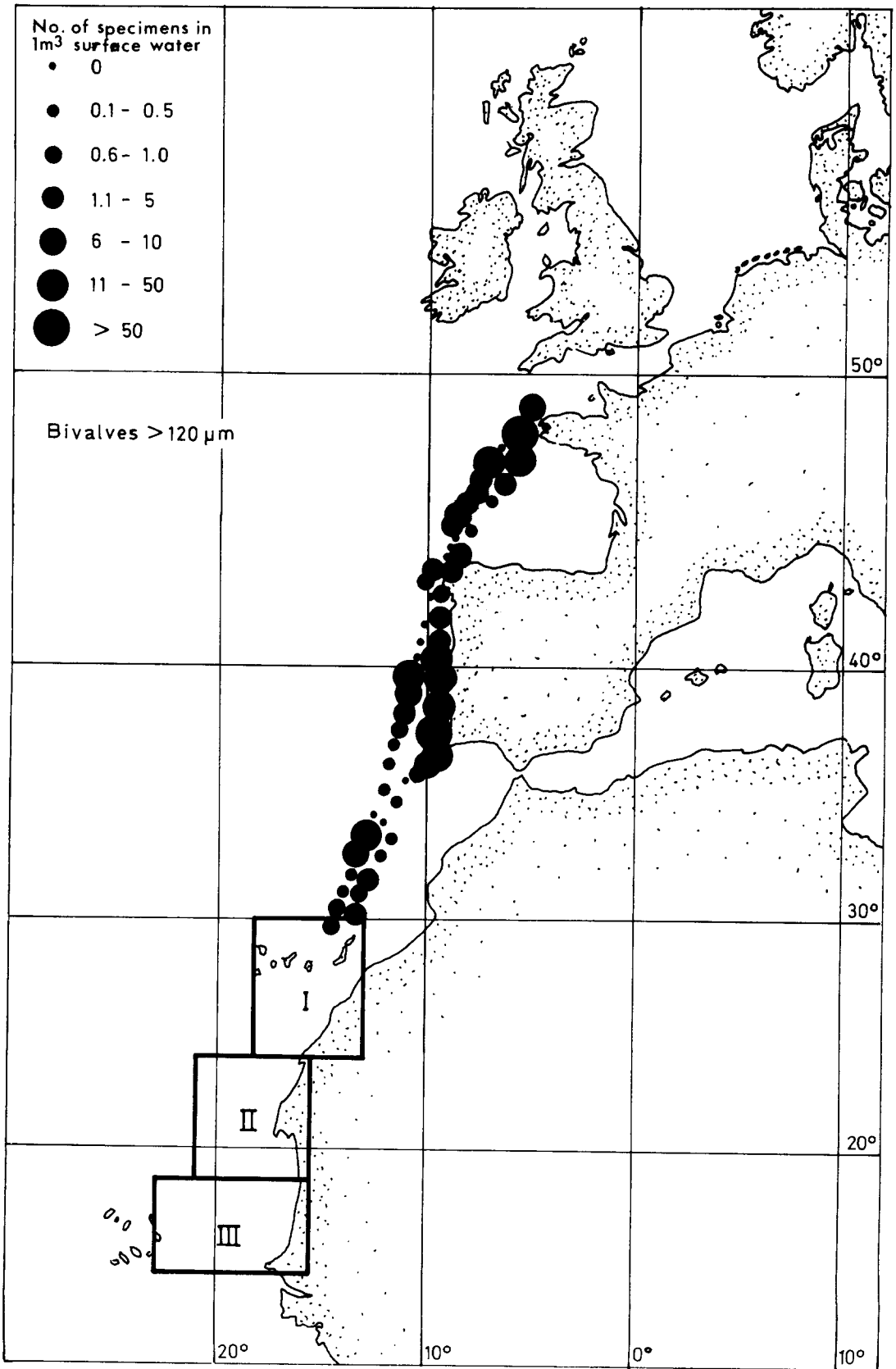


Fig. 2B. (Legend see p. 276.)

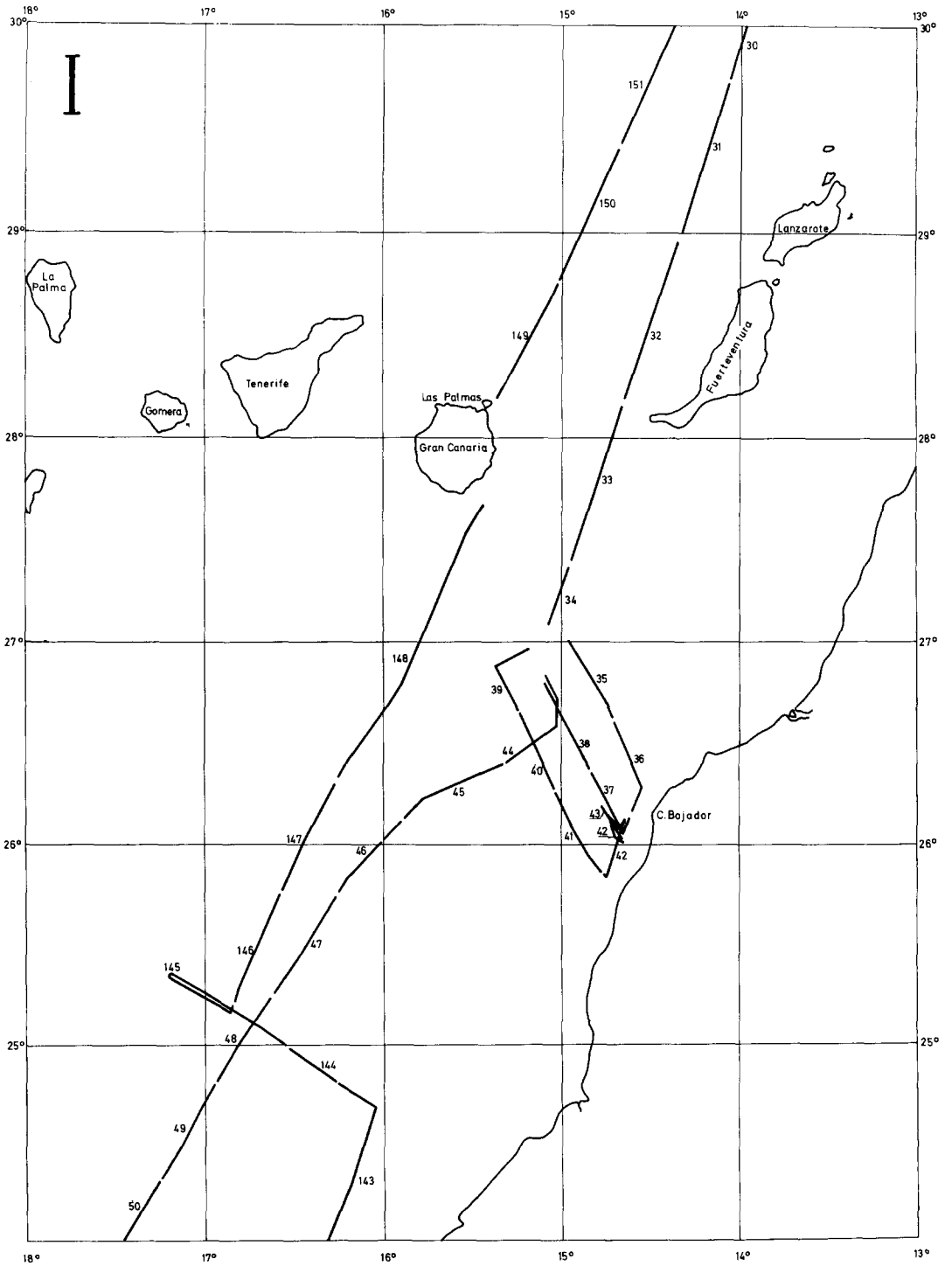


Fig. 2AI. (Legend see p. 276.)

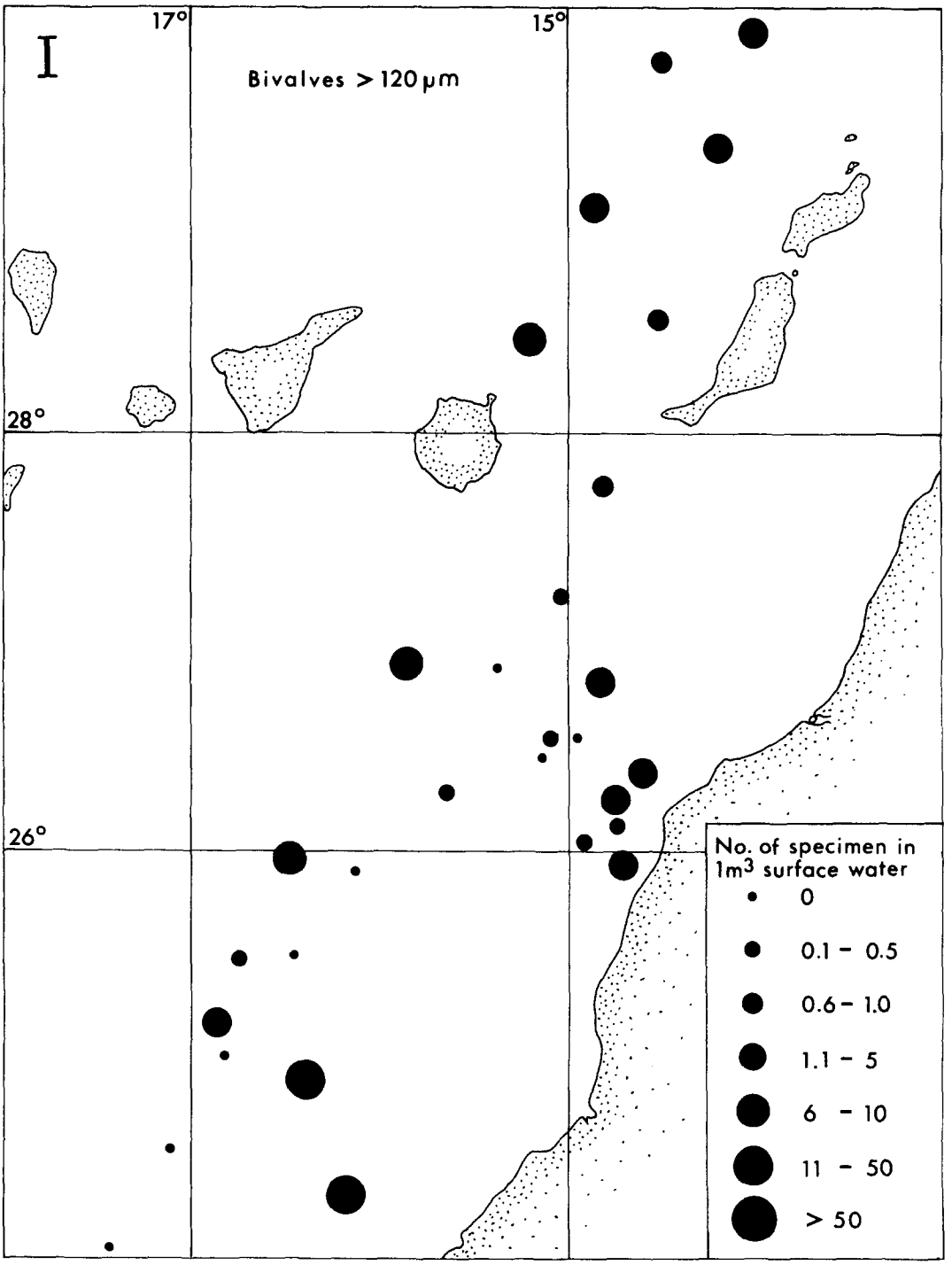


Fig. 2BI. (Legend see p. 276.)

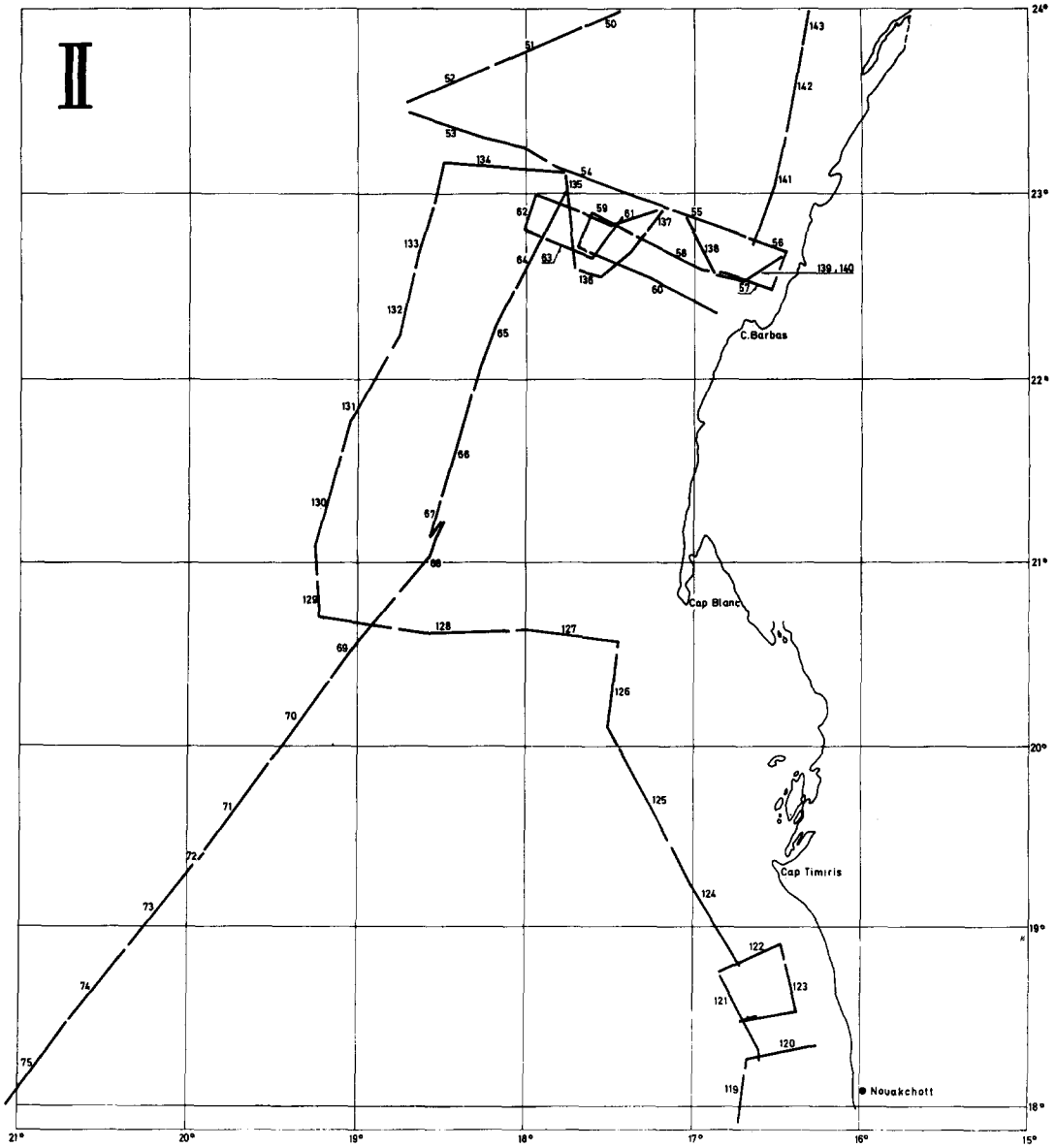


Fig.2AII

Fig. 2. Distribution of mero-planktonic larval shells of bivalves in eastern North Atlantic surface-water masses. Sample locations are found in Fig. 2A, the quantitative distribution (expressed in number of specimens > 120 μm per 1 m^3 surface water) in Fig. 2B. The areas I, II and III are shown on more detailed maps.

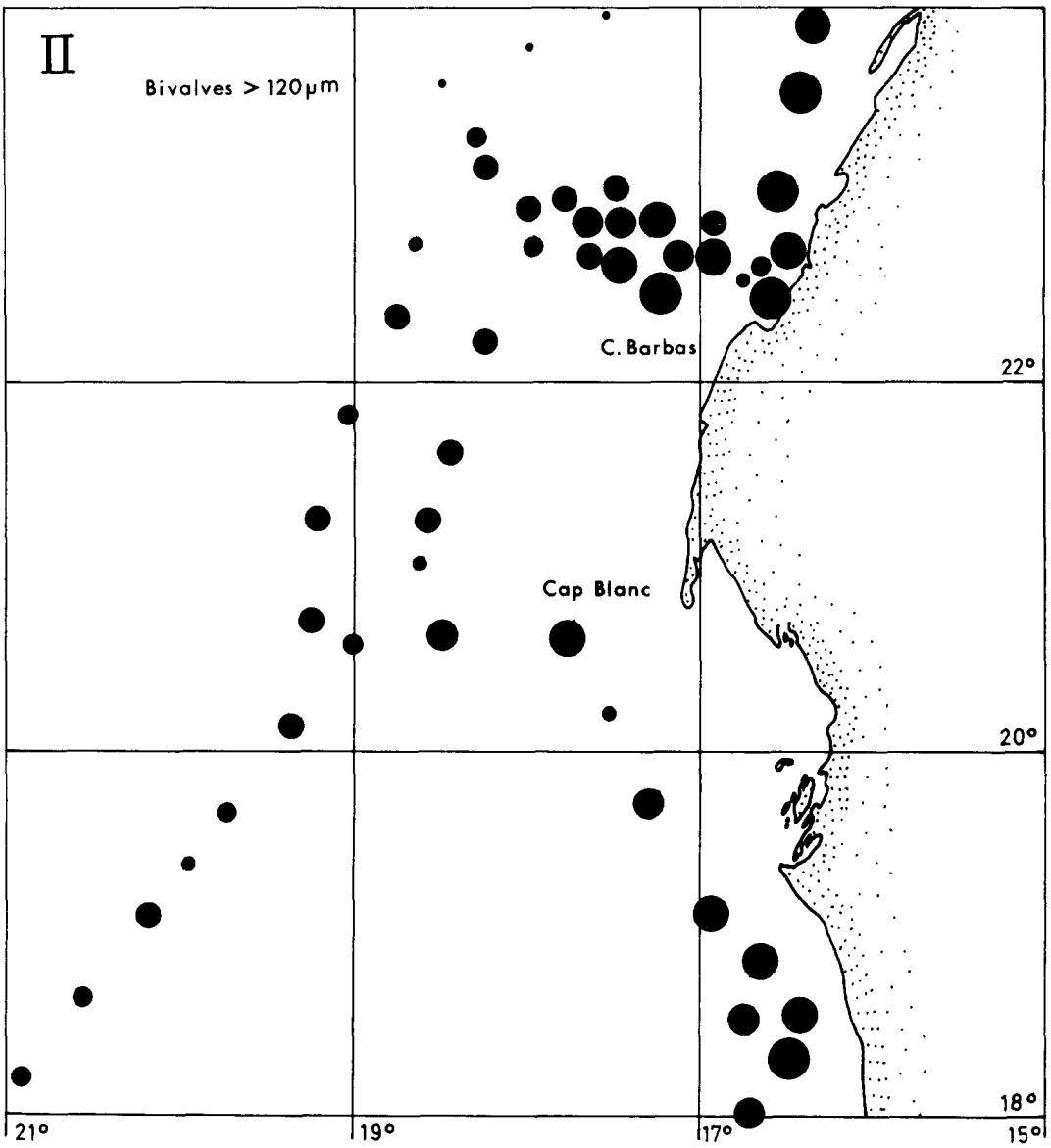


Fig.2BII

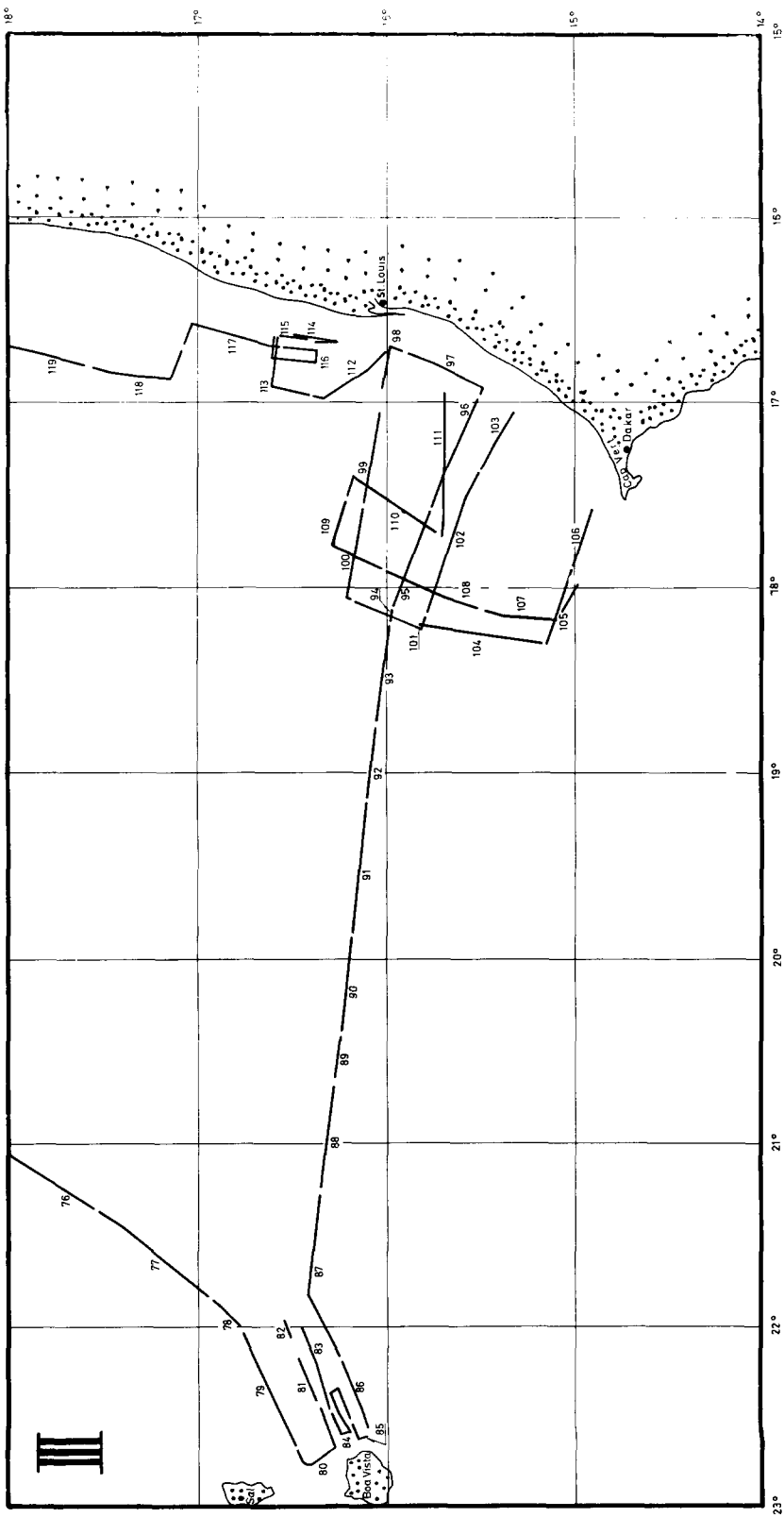


Fig. 2AIII. (Legend see p. 276.)

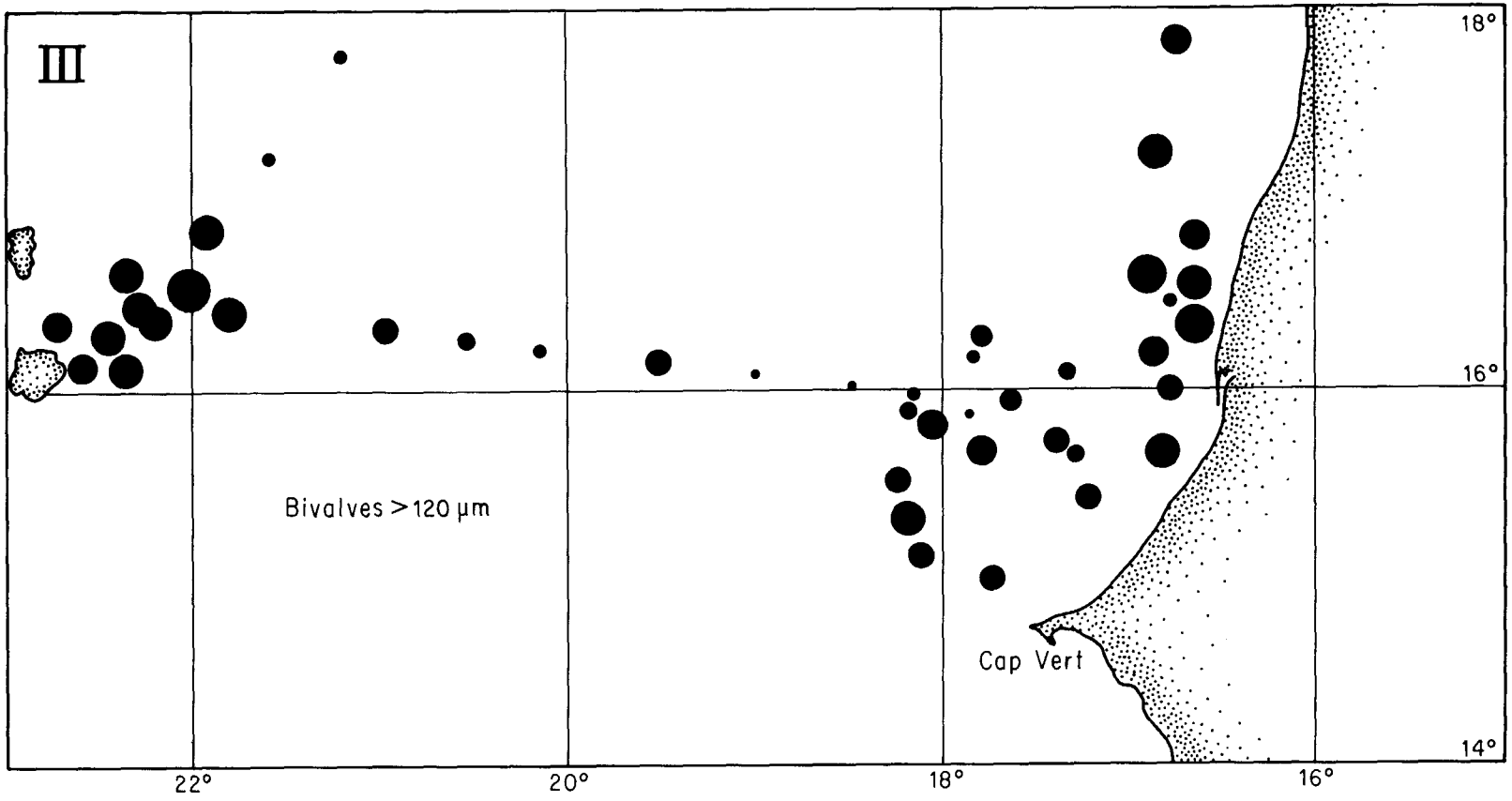


Fig. 2BIII. (Legend see p. 276.)

Africa during this cruise, samples have been taken not only in the open ocean, but also in coastal waters (as shown for the plankton samples obtained by pumping surface water, in Fig. 2A). Samples to study the living assemblages of planktonic organisms which possess shells or tests, and which later are expected to contribute these components as fossils to the sediments, have been obtained with two different devices:

(1) Surface water from about 4 m water depths (mouth of pump) has been pumped through a filter set with mesh sizes of 120, 250 and 1010 μm. The amount of filtered water could be controlled by a water meter. On the average, about 6 m^3 of water have been filtered for each sample. In almost all samples only the two smaller fractions contained a sizeable number of shells and tests.

(2) At a number of stations a plankton net (multiple Simonsen-net, 40 μm mesh size, compare Dietrich et al., 1966) has been used for tows from maximum water depths of up to 600 m (depending on the total water depth) in a maximum of eight different depth intervals (as indicated for the two stations mentioned in this paper in Tables I and II).

The quality of the samples has been controlled on board with an Utermöhl plankton microscope. Most bivalve larvae were found living; however, singular empty shells occurred here and there. All samples have been preserved with carefully buffered formalin. To separate shells, tests and skeletons from the abundant planktonic organisms without these (mainly pelagic crustaceans), the method of Sachs et al. (1964), although somewhat modified, has been used. They have proposed ignition of plankton samples in a combustion furnace as a means of concentrating shell-bearing organisms, which usually only occur as accessory components together with large quantities of soft-bodied organisms. Heating the furnace over 450—480° C was carefully avoided. The components have then been counted under a normal micropaleontological stereomicroscope (reflected light).

Since it seems impossible at the present stage of the study to determine the bivalve species which are actually contributing to the larval shell assemblages, it was difficult to choose a parameter as a valid size measure for these shells. However, it is the intention to compare these samples with data from sediment coarse fractions of the same area. Therefore, it seemed important to choose a parameter which could be reproduced fairly easily by sieving the samples. Such a parameter is normally the medium axis of a triaxial grain. With respect to the bivalve shells described here this is usually the vertical axis. In addition, many shells have an almost round disc-like shape resulting in nearly equal long axes which lie parallel to the symmetric plane between the shells.

A detailed account of these laboratory procedures and the complete set of data obtained from the above-mentioned samples (including the abundances of all other shell- and test-bearing planktonic organisms such as diatoms, radiolaria, foraminifera, gastropods, ostracodes, etc.) are in final preparation and will be published in the very near future in the scientific reports of "Meteor" (Thiede, 1974)

TABLE I

Location data of multi-net plankton tows off Cape Barbas (West Africa)

Sample no.	Position	Total water depth (m)	Sampled water depth (m)	No. of sampled depth intervals
12322—1	22°54.2'N 17°09.8'W	307	280	6
12326—1	23°02.1'N 17°24.6'W	1013	600	7

TABLE II

Diameter (mm) of largest and smallest bivalve shell at different water depths (m) off Cape Barbas (West Africa; see Table I)

Sample no.	Sampled water depth (m)	No. of specimen measured	Diameter (mm)		
			Mean	Largest shell	Smallest shell
12326—1	0—25	18	0.163	0.26	0.09
	25—50	11	0.176	0.19	0.13
	50—100	4	0.141	0.18	0.14
	100—200	5	0.138	0.16	0.13
	200—550	no measurable specimen			
	550—600	1		0.49	
12322—1	0—25	108	0.126	0.34	0.09
	25—50	7	0.139	0.18	0.09
	50—100	34	0.119	0.20	0.08
	100—200	183	0.115	0.20	0.08
	200—240	101	0.105	0.35	0.09
	240—280	35	0.120	0.19	0.09

QUANTITATIVE DISTRIBUTION IN EASTERN NORTH ATLANTIC SURFACE WATER MASSES

In Fig. 2B the quantitative distribution of bivalve shells is shown expressed in number of specimens per filtered cubic meter of surface water. The numbers obtained from the original two or three size fractions have been added and are given here as numbers of bivalves larger than 120 μm. These distributions will be treated in the forthcoming paragraphs under the following aspects: differences between tropical, subtropical and temperate areas, differences between samples taken close to or far from shelf and shallow-water areas, and effects of upwelling.

Differences North—South

The bivalve larvae seem to be distributed equally in the eastern North Atlantic south of 50°N, in terms of climatic zonation (Mileikovsky, 1968).

However, this can be evaluated only with difficulty since the ship's course while taking these samples crossed areas of the ocean very close to land and far out in the ocean (see Fig.2A). This sometimes implies rather large distances from areas where larvae can be produced (after Thorson, 1950; mainly shallow-water shelf areas), thus possibly causing abundance fluctuations.

Differences between open ocean and shelf areas

The difference in abundance found close to land and far from the coast is very clearly expressed in all series of samples which run perpendicular to continental or island margins out into the pelagic environment of the ocean and vice versa. Good examples of this trend have been found off western France, Spain, Portugal and West Africa, whereas these differences are less well expressed off Cape Bojador, but very well expressed off Cape Barbas and in the whole region between Cape Barbas and Cape Vert.

A very interesting feature is the isolated high abundance of bivalve larvae close to the Cape Verde Islands which can only be understood by accepting that bivalve faunas of these island shelves produce their own larvae. These values of high abundance are limited to the north and east by rather small values, the only directions from whence considerable continental-margin contributions of larvae could be expected because of the pattern of surface currents in this region (Deutsches Hydrographisches Institut, 1967).

High abundances have also occasionally been found far from land, for example, southwest of Cape San Vincent (Portugal). There are several possibilities to explain the presence of these larvae. They could have been produced in the shallow areas off the Iberian Peninsula. Since a number of samples close together yielded high abundances, these values seem not to be found accidentally but appear rather to indicate that the larvae are present as large swarms in the surface water. When these water masses are removed from the shelf area, they transport their larval communities out into the ocean. Another possibility is offered by the presence of a certain number of submarine mountains in this area, for example Goringe Bank, Ampère Bank, Josephine Bank, and Seine Bank. Several of these volcanic peaks reach very shallow water depths and are covered by biogenic calcareous rocks and loose sediment (Closs et al., 1969). Bivalve faunas living on these shallow summits can only have come there due to the displacement of larvae from other areas, and they are thus also expected to produce larvae which can be carried further on.

Upwelling regions

The region between Cape Barbas and Cape Vert is especially characterized by upwelling phenomena causing high fertility of the water masses close to the coast (Weichart, 1970). It seems clear from Fig. 2B that this area is also set off by the abundance of bivalve larvae found in the samples close to land in

this area (Fig. 2B, II and III; compare also Allen and Scheltema, 1972). Frequencies off Cape Bojador, where upwelling is less intensive, are considerably smaller.

However, the samples taken close to the Cape Verde Islands and those off Portugal and western France have yielded similar numbers of bivalve larvae and it is therefore not quite clear if upwelling is the only cause. This may mainly apply to tropical and subtropical areas where reproduction takes place without major interruptions due to seasonal changes (Thorson, 1950; Seguin, 1966). Seasonal variations of water temperature might, at least in the northern part of the studied area, affect larval abundances as well.

QUANTITATIVE DISTRIBUTION IN THE WATER COLUMN

Hitherto only samples from the surface water masses have been considered. The few available vertical plankton multi-net tows have revealed interesting patterns of depth distributions of bivalve larvae. From the available stations two plankton tows off Cape Barbas have been selected for Fig. 3, 12326—1 being taken far from land over the deep sea, and 12322—1 close to land in a water depth of a few hundred meters.

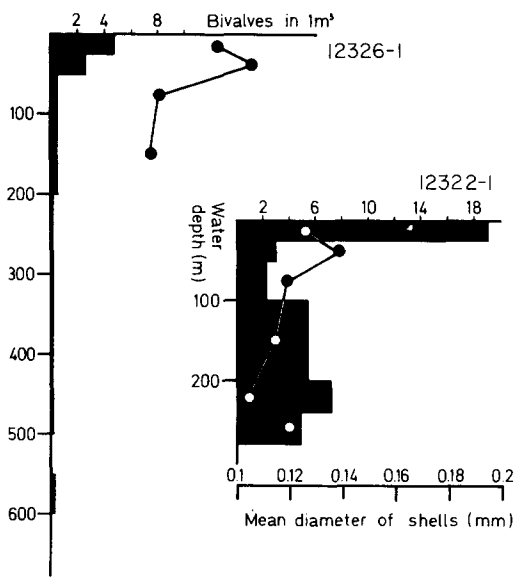


Fig.3. Plankton multi-net tows off Cape Barbas (West Africa). The vertical distribution of bivalve shells (> 40 μm) is expressed in average number of specimens in 1 m^3 of filtered water in the sampled depth intervals. The average diameter of shells in these samples is indicated by curves (points are only given if enough specimens have been found). Station 12326—1: 0—600 m; 12322—1: 0—280 m (compare Tables I and II).

Bivalve shells have been found less frequently in 12326—1 because of its greater distance from land. In both series the interval 0—25 m water depth yielded the bulk of bivalve larvae, whereas the frequency decreased drastically in the samples below this depth. While this trend could be followed in the deep-water tow down to 600 m water depth, the abundance of bivalve shells again increases at the shallow station below 100 m water depth.

SIZE DISTRIBUTION

The size distribution of bivalve larvae varied systematically. The percentage of larvae in the coarser fraction (250—1010 μm), as compared to the total shell assemblage (120—1010 μm), increased with increasing distance from land. Usually small larvae were concentrated above the shelf close to land or above submarine elevations.

Several samples were measured in greater detail; one series off Cape Blanc and one off western France have been selected for Figs. 4A and 4B. In both series most shells are 0.2—0.3 mm in size, except samples 129 and 174, which have in common that they have been taken far from land. Samples 127, 128 and 129 (Fig. 4A), which run almost perpendicular to the shelf, illustrate that the small-size bivalve shells decrease in number in favor of the larger ones with increasing distance from the coast. At the same time, the absolute frequency of shells decreases drastically in the same direction. The increase of size with increasing distance from land is less evident in the series of samples off western France (Fig. 4B), but is still visible. The same trend has also been found in the two plankton tows illustrated in Fig. 3 where only the average diameter of shells in the sampled depth intervals (only if enough specimens were available) is given.

The vertical size distribution of larval shells observed in both tows (Fig. 3) revealed that shells with the largest mean diameter are found in 25—50 m water depth, while the mean shell diameter above, and especially below these depths, becomes smaller. However, the largest shell was found in station 12326—1 in 550—600 m water depth (Table II). It seems remarkable that this trend of depth zonation is similar at both stations, although the mean shell diameter is much larger in the samples from the deep-water station. It might be reasonable to search in the specific larval development for an explanation of this phenomenon; however, this cannot be attempted here because of missing species determinations. The significance of the above-mentioned trend will be further evaluated after measuring all available plankton tows.

DISCUSSION AND CONCLUSIONS

One of the first problems to solve was the source of these larvae, since mollusc larvae can possibly be transported across the ocean (Scheltema, 1966, 1971a, b). It was therefore important to prove that these bivalve larvae had

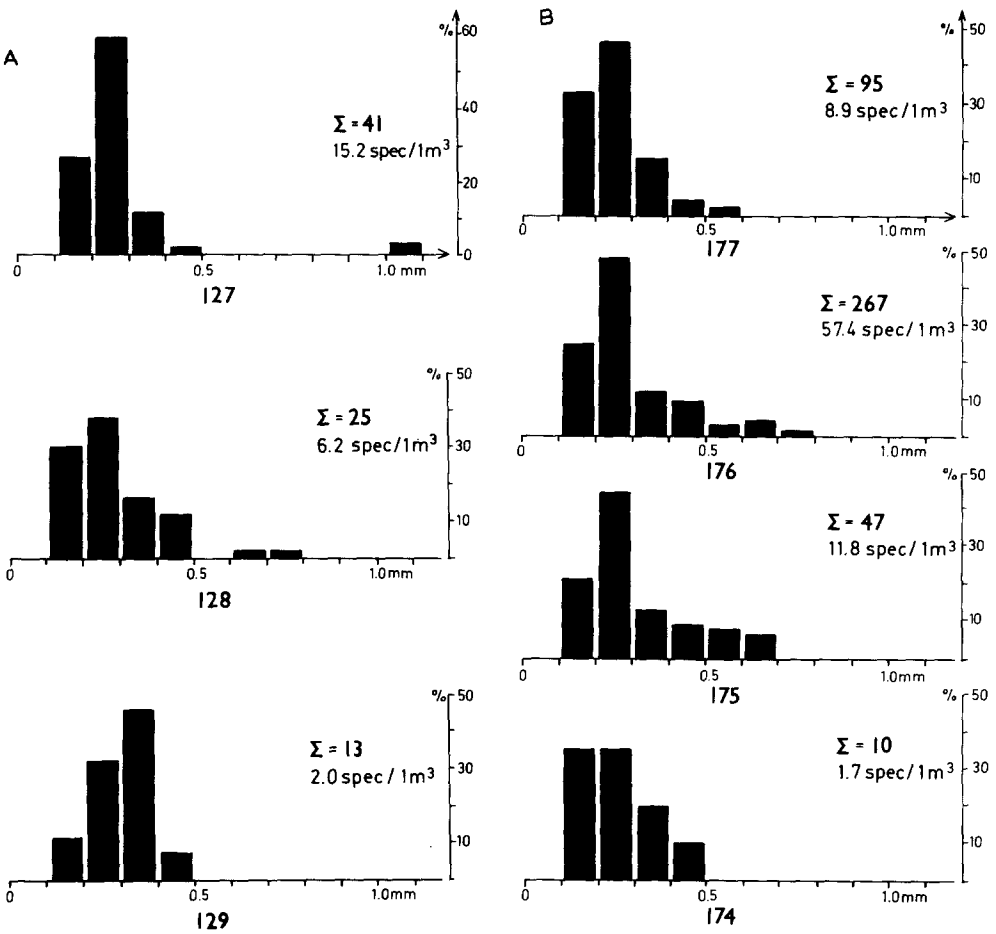


Fig.4. Size distributions of bivalve shells in surface water plankton samples arranged according to increasing distance from land (compare Fig.2 for sample locations).
A. Samples off Cape Blanc (West Africa). Sample 127 has been taken in coastal waters, sample 128 in intermediate, and sample 129 in water masses far from land.
B. Samples taken in the northern Bay of Biscay, off Brittany (France) and in the entrance to the English Channel. Sample 174 has been filtered far from land from surface waters of the Bay of Biscay, sample 177 in the entrance of the Channel.

not been brought across the Atlantic Ocean by the southern branches of the Gulf Stream system (Sverdrup et al., 1942) from the East Coast of North America. Two arguments seem to serve as the solution of this problem, namely frequency distribution and size distribution. Larvae should occur most abundantly nearest their area of origin and they should be smallest there as well. With increasing distance from this area, their frequency should diminish. With

these arguments in mind, three principally different types of sources for larvae can be pointed out, where bivalve or, in general, mollusc faunas are known to occur:

(a) marginal areas of continents such as shelves and possibly the uppermost part of the continental slope;

(b) marginal areas of islands;

(c) summits of submarine elevations, which approach the oceanic water surface (guyots, other types of submarine mountains, etc.).

These three possibilities of regional sources of bivalve larvae have been confirmed by the present study, Type a being represented by the continental margin of western France, the western Iberian Peninsula and West Africa, Type b by the Cape Verde Islands and Type c by the submarine elevations between southwestern Portugal and the Canary Islands.[1]

At first, a trend of increasing abundances of bivalve larvae from north to south was expected to be found (Thorson, 1946), since it is known that the percentage of benthic mollusc species (both gastropods and bivalves) with a pelagic larval stage increases from north to south in the Northern Hemisphere (Fig. 5A and B, after Thorson, 1950 and Ockelmann, 1965). However, no higher abundances have been found, presumably because of the fact that most of the bivalve species (over 80%) with known larval development already develop pelagic larvae in the northern area covered by the studied samples.

For the determination of the region of origin it seems also important to know that most bivalves known to have a pelagic larval stage live in shallow waters, a trend which increases to the north (compare Fig. 6, after Ockelmann, 1965: He defines planktotrophic = with long pelagic life and feeding on plankton; lecithotrophic = with short pelagic life, feeding from large yolky eggs, and non-pelagic larval development after Thorson, 1950). Ecological similarities of the deep-sea and polar shallow-water areas help to understand the "equatorial submergence" of many polar shallow-water bivalves, thus explaining the scarcity of bivalve larvae in greater water depths (Thorson, 1950; Scheltema, 1972). An extreme limit of a few hundred meters of water depth for the breeding of such species also exists in tropical areas since almost all larvae are photopositive during part of their larval development, forcing them to ascend to the water surface (Thorson, 1950).

The fact that these larvae are photopositive for a large part of their existence (because of being at least partly phytoplanktotrophic, Scheltema, 1971c) and that they are produced in the upper few hundred meters of the water column might explain their frequency distribution as well as their size distribution (Fig. 3). The large specimen found in deep water could be explained as a relatively old larva, which has become photonegative (Thorson, 1950) and which is searching for a suitable substrate to settle on.

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[1] Living faunas on submarine mountains should be investigated if they consist of mollusc species with a pelagic larval development. Otherwise it would be very difficult to explain the presence of mollusc faunas on top of guyots.

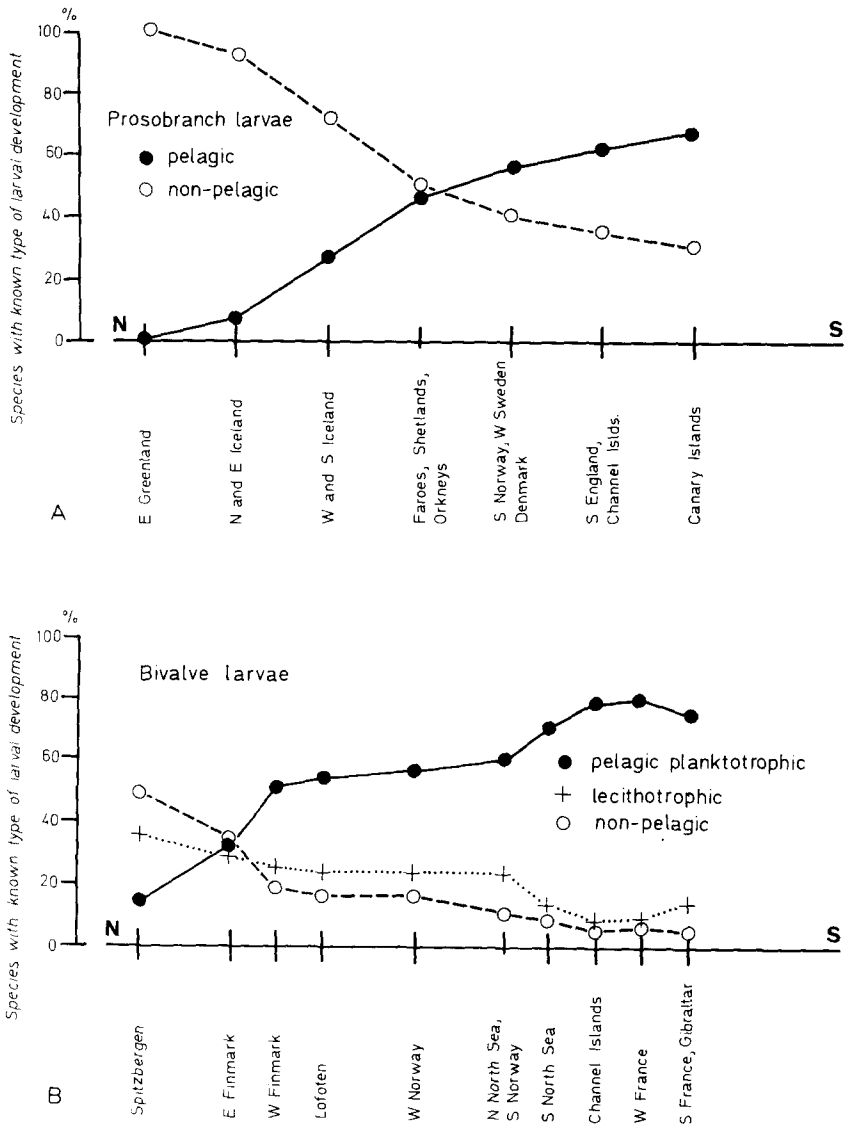

Fig.5. Distribution of mollusc species with known type of larval development arranged on N—S profiles.

A. Prosobranchs (after Thorson, 1950). The profile has its extremes in eastern Greenland and at the Canary Islands, thus spanning from holarctic climatic zones to sub-tropical ones. The species have been divided into those which do not have a pelagic larval stage and those producing mero-planktonic veliger.

B. Bivalves (after Ockelmann, 1965). Profile spans from lusitanic to holarctic climate zones. Three types of larvae have been discerned: pelagic planktotrophic ones, lecithotrophic ones with a short pelagic larval stage, and non-pelagic ones (compare text).

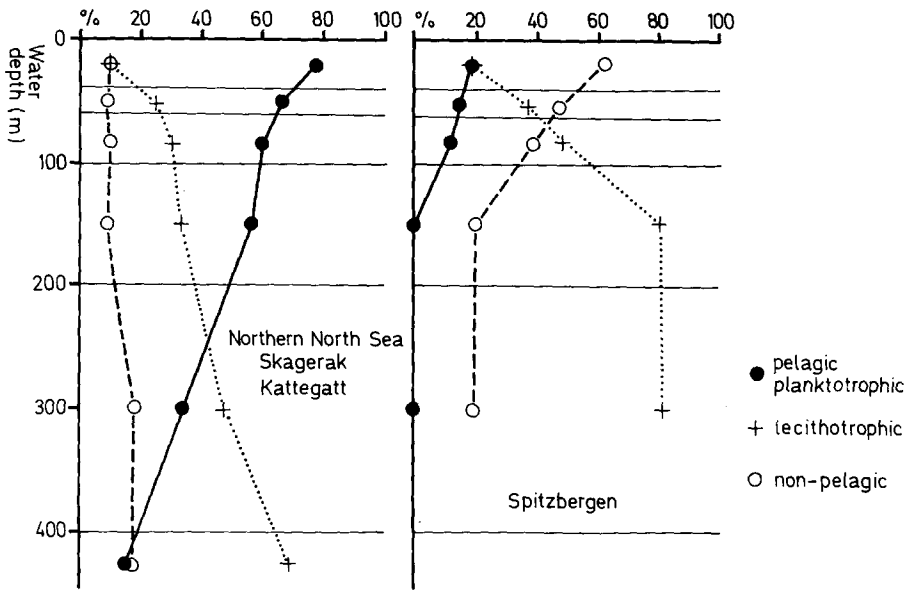

Fig.6. Depth distribution of bivalve species with known type of larval development (after Ockelmann, 1965). As in Fig. 5 three types of larval development have been discerned: pelagic planktotrophic, lecithotrophic with a short pelagic larval stage, and non-pelagic (compare text). Examples for holarctic and boreal faunas are given.

The above-mentioned considerations have broad paleogeographic implications, since the mechanism of development of pelagic larvae can be expected to rule the regional distribution of a large proportion of mollusc species. This might be especially evident at narrow entrances from the ocean to marginal seas (for example, the Straits of Gibraltar, the entrance to the Red Sea, the Persian Gulf and the Black Sea) or connections between oceans, as in Tertiary times between the Pacific and the Atlantic Oceans. The manner of water exchange through these entrances is usually controlled by climatic conditions (Dietrich, 1957; Defant, 1961; Seibold, 1970), an arid climate causing a surface water inflow and a bottom water outflow (Strait of Gibraltar, Bab el Mandeb, Strait of Hormuz), and a humid climate resulting in a surface water outflow and a bottom water inflow (Kattegatt and entrances to Baltic Sea). This mechanism will presumably slow the immigration of molluscs into marginal basins under subpolar to temperate humid conditions (except in polar regions, Seibold, 1970). Basins in arid regions (usually close to tropical climatic belts) will be populated very rapidly after the connection to the ocean has been established. Tropical humid conditions would not affect the distributions of molluscs with pelagic larvae since these live down to depths of several hundred meters (compare Fig. 3,6). However, under all conditions, a selective influence might be expected because the larval stage of development is usually the stage with most limiting environmental requirements for an animal.

ACKNOWLEDGEMENTS

I would like to thank E. Seibold, Kiel, for having invited me on board "Meteor" during cruise no. 25, and for his helpful suggestions and current interest. G. Wefer (Kiel), D. Herm (Tübingen), and O. B. Nielsen (Aarhus) helped in sampling on board, while the filter set was borrowed from J. Lenz (Kiel). Mrs. Jette Grejs Pedersen (Aarhus) assisted carefully with the laboratory procedure of these samples. The English text has been corrected by E. R. Stevens. I acknowledge the comments of P. Chanley (Greenport, N.Y.) and R. S. Scheltema (Woods Hole, Mass.). This study has been supported by the German and the Danish Research Societies.

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